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[Article]

Behavioral Thermoregulation and Slowed Migration by Adult Fall Chinook Salmon in Response to High Columbia River Water Temperatures

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Abstract.—The relationships between lower Columbia River water temperatures and migration rates, temporary tributary use, and run timing of adult fall Chinook salmon *Oncorhynchus tshawytscha* were studied using historical counts at dams and recently collected radiotelemetry data. The results from more than 2,100 upriver bright fall Chinook salmon radio-tagged over 6 years (1998, 2000–2004) showed that mean and median migration rates through the lower Columbia River slowed significantly when water temperatures were above about 20°C. Slowed migration was strongly associated with temporary use of tributaries, which averaged 2–7°C cooler than the main stem. The proportion of radio-tagged salmon using tributaries increased exponentially as Columbia River temperatures rose within the year, and use was highest in the warmest years. The historical passage data showed significant shifts in fall Chinook salmon run timing distributions concomitant with Columbia River warming and consistent with increasing use of thermal refugia. Collectively, these observations suggest that Columbia River fall Chinook salmon predictably alter their migration behaviors in response to elevated temperatures. Coolwater tributaries appear to represent critical habitat areas in warm years, and we recommend that both main-stem thermal characteristics and areas of refuge be considered when establishing regulations to protect summer and fall migrants.

Efforts to manage, conserve, and restore populations of anadromous salmonids in the western USA and Canada have increasingly focused on reestablishing the functional processes of the freshwater ecosystems on which they depend. Unfortunately, freshwater habitats and lotic systems, in particular, are highly vulnerable to alterations caused by competing water uses (Malmqvist and Rundle 2002). Development in watersheds, irrigation withdrawals, reductions of riparian cover, and impoundment and flow management for hydropower generation, flood control, and navigation have all measurably increased thermal inputs to aquatic systems. Rising temperatures can strongly affect species distributions and persistence (Poff et al. 2002), and these effects will be compounded under predicted scenarios for regional climate change (Mote et al. 2003). Better predictions of how aquatic populations respond to river warming require an understanding of the behavioral plasticity that exists within individual populations and species. Anadromous salmonids represent ideal study subjects to address this question because of their reliance on and sensitivity to water quality during multiple life cycle stages. Here, we examine the migration behavior and timing of homing adult salmon and discuss their prospects for behaviorally adapting to a rapidly warming migration environment.

Anadromous salmonids are widely distributed and have evolved some of the more complex migration strategies of any group of organisms (Dingle 1996; Dodson 1997). Among salmonids, Chinook salmon *Oncorhynchus tshawytscha* exhibit some of the greatest variation in their migration tactics. In the Sacramento River, for example, four runs of Chinook salmon (spring, fall, late fall, and winter) are recognized, while in the Columbia River, there are three distinct runs (spring, summer, and fall), distinguished by season of freshwater entry, spawning distribution and timing, and

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juvenile behavior. Run timing appears to be governed by a combination of travel distance and long-term discharge and water temperature regimes in the migration corridor and on spawning grounds (Groot and Margolis 1991; Quinn and Adams 1996; Dodson 1997; Quinn et al. 2000; Quinn 2005). In the Columbia River, many adult spring and summer Chinook salmon migrate long distances to natal streams in headwater areas and enter freshwater many months prior to fall spawning season (stream type; Healey 1983). As a result these populations primarily migrate prior to the onset of warm water conditions in the migration corridors (Keefer et al. 2004b). In contrast, adult fall Chinook salmon (ocean type) typically initiate migration near peak summer temperatures and during the fall cooling phase of the temperature cycle (Healey 1983; Coutant 1999; Brannon et al. 2004). Migration in the lower Columbia River occurs from midsummer through October before spawning in October and November (Dauble and Watson 1997; Myers et al. 1998). The fall run is composed of two main groups: (1) those that spawn in the lower river and its tributaries up to about river kilometer (rkm) 308, and (2) the upriver bright (URB) fall Chinook salmon (Howell et al. 1985), the group of interest in our study. Most remaining URB fall Chinook salmon spawn in or upstream from the Hanford Reach (Figure 1), the last unimpounded section of the Columbia River upstream from Bonneville Dam (Dauble and Watson 1997); there are smaller populations in the Deschutes and Yakima rivers, and a remnant population that returns to the Snake River basin. Snake River fall Chinook salmon were listed as threatened under the Endangered Species Act in 1992 (NMFS 1992).

The impoundment of the lower Columbia and Snake rivers by a series of hydroelectric projects (Figure 1) and the resulting flow manipulations have correlated with a trend of warmer water temperatures within the system (Quinn et al. 1997). Over the last several decades, the main stem has steadily warmed earlier in the spring and cooled later in the fall (Quinn and Adams 1996). Warming due to impoundment and water diversion has been exacerbated by regional climate change. Since 1948, air temperatures have increased significantly (>1°C) in much of the Pacific Northwest area of the United States (Lettenmaier et al. 1994; Hamlet and Lettenmaier 1999). Recent August and September water temperatures in the Columbia River have averaged 20–21.5°C, with maximum daily highs of up to 24°C (i.e., USACE 2004). Optimum temperatures for migrating adult Chinook salmon are thought to be between 10.5°C and 19.5°C, and migrations may be blocked in the range of 19–23°C (Bell 1986; McCullough et al. 2001; Richter and Kolmes 2005). The incipient lethal limit for jack fall Chinook salmon is 21–22°C (Coutant 1970), and the critical thermal maximum for the species is 25°C (Bell 1986).

We investigated how fall Chinook salmon have responded to altered temperature conditions and specifically to what degree fall Chinook salmon may adjust their run timing and upstream progression when encountering warmwater conditions. Our analysis had two components. First, we examined run timing characteristics of fall Chinook salmon at the four Lower Columbia River dams using available historical data. Because we expected salmon to avoid high water temperatures when possible, we predicted that more recent fall runs would arrive either earlier or later than the long-term average in response to warming of the lower Columbia River. Earlier timing might be expected for some fish because migration rates are higher at moderately warmer temperatures (Keefer et al. 2004a), while later timing may occur if fish delay or stop migration in response to high temperatures. Second, we hoped to identify where and how fish responded to high water temperatures and to quantify resulting migration behavior. These objectives were addressed using passage rate and behavior data collected for more than 2,100 radio-tagged URB adult fall Chinook salmon. One behavior of particular interest was the temporary use of coolwater tributaries by migrants destined for upstream spawning areas. We hypothesized that temporary use of tributaries could reflect beneficial thermoregulation, but could also be a mechanism for run delays and shifts in migration timing.

Study Site

The study area encompassed 404 km of the Columbia River from Bonneville Dam (rkm 235) upstream to Priest Rapids Dam (rkm 639) and Ice Harbor Dam (rkm 538) on the Snake River (Figure 1). This section of the Columbia River hydrosystem has a mean annual discharge of 5,520 m^3/s (Favorite et al. 1976), six hydroelectric projects, and 13 major tributaries. Tributary streams large enough to be used by adult salmon in the lower segment of river (downstream from John Day Dam, rkm 347) were Eagle Creek, Herman Creek, and the Wind, Little White Salmon, White Salmon, Hood, Klickitat, and Deschutes rivers.

Methods

Historical run timing.—Daily fall Chinook salmon counts at dams, collected by the U.S. Army Corps of Engineers (USACE), were used to calculate median and quartile passage dates of annual runs at Bonneville

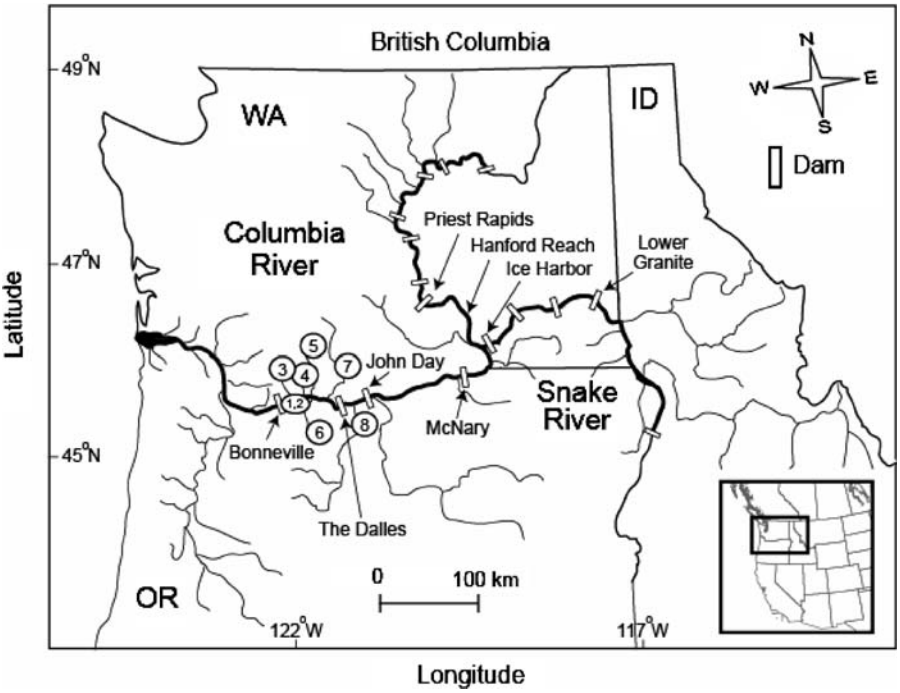

FIGURE 1.—Map of the Columbia River study location, including the migration corridor used by upriver bright fall Chinook salmon, the fish collection location (Bonneville Dam; rkm 235), and tributaries where temporary use was monitored. Tributaries include: (1) Eagle Creek, (2) Herman Creek, (3) Wind River, (4) Little White Salmon River, (5) White Salmon River, (6) Hood River, (7) Klickitat River, and (8) Deschutes River.

(1938–2004), the Dalles (1957–2004), John Day (1968–2004), and McNary (1954–2004) dams. Run totals were calculated from 1 to 9 August through 31 October at each dam based on established run separation dates in USACE annual fish passage reports (USACE 1938–2004). Years with incomplete data (most frequent at the Dalles Dam) were excluded. We used linear regression to assess correlations between year and median passage date, quartile dates, and interquartile ranges at the four dams.

Radio tagging and telemetry monitoring.—Radio tagging occurred in the adult fish facility adjacent to the Washington shore fishway at Bonneville Dam. Fish migrating upstream were diverted from the fish ladder into the trap each morning, scanned for passive integrated transponder (PIT) tags implanted when fish were juveniles (4% of the 2000–2004 sample had juvenile PIT tags), and passed into an anesthetic tank containing clove oil or tricaine methanesulfonate. Anesthetized salmon were inspected for injuries and fin clips, sexed, and measured. Radio tags (coated with glycerol to aid insertion) were gastrically implanted with a small wire antenna protruding from the mouth. One of three tags were used: (1) 7 V (8.3 cm long × 1.6 cm diameter, 13 g in water), (2) 3 V (4.5 × 1.3 cm, 4.1 g in water), or (3) 3 V archival (9 × 2 cm, 20 g in water; Lotek Wireless, Newmarket, Ontario). Following radio tagging, PIT tags were injected near the left pelvic fin of fish without PIT tags (2000–2004) or a visual implant tag was inserted just beneath the exterior lens of either eye (1998). Fish were placed into a 2,270-L aerated recovery tank fixed to a trailer and driven to release sites downstream from Bonneville Dam at sites on both sides of the Columbia River. Tagging was broadly proportional to passage over Bonneville Dam and began on 1 August and continued through early to mid-October (Figure 2). In 1998 and 2004, however, tagging was delayed due to high water temperatures. Additional research priorities in other years precluded strictly proportional sampling. A total of 4,364 salmon were tagged (annual range = 561–1,032 fish), representing less than 1% of each run counted at Bonneville Dam.

Transmitters emitted a unique digital code on frequencies between 149.480 and 149.800 MHz and movements were monitored using a series of radio receivers with aerial antennas stationed in the tailraces of dams from Bonneville Dam upstream to Lower

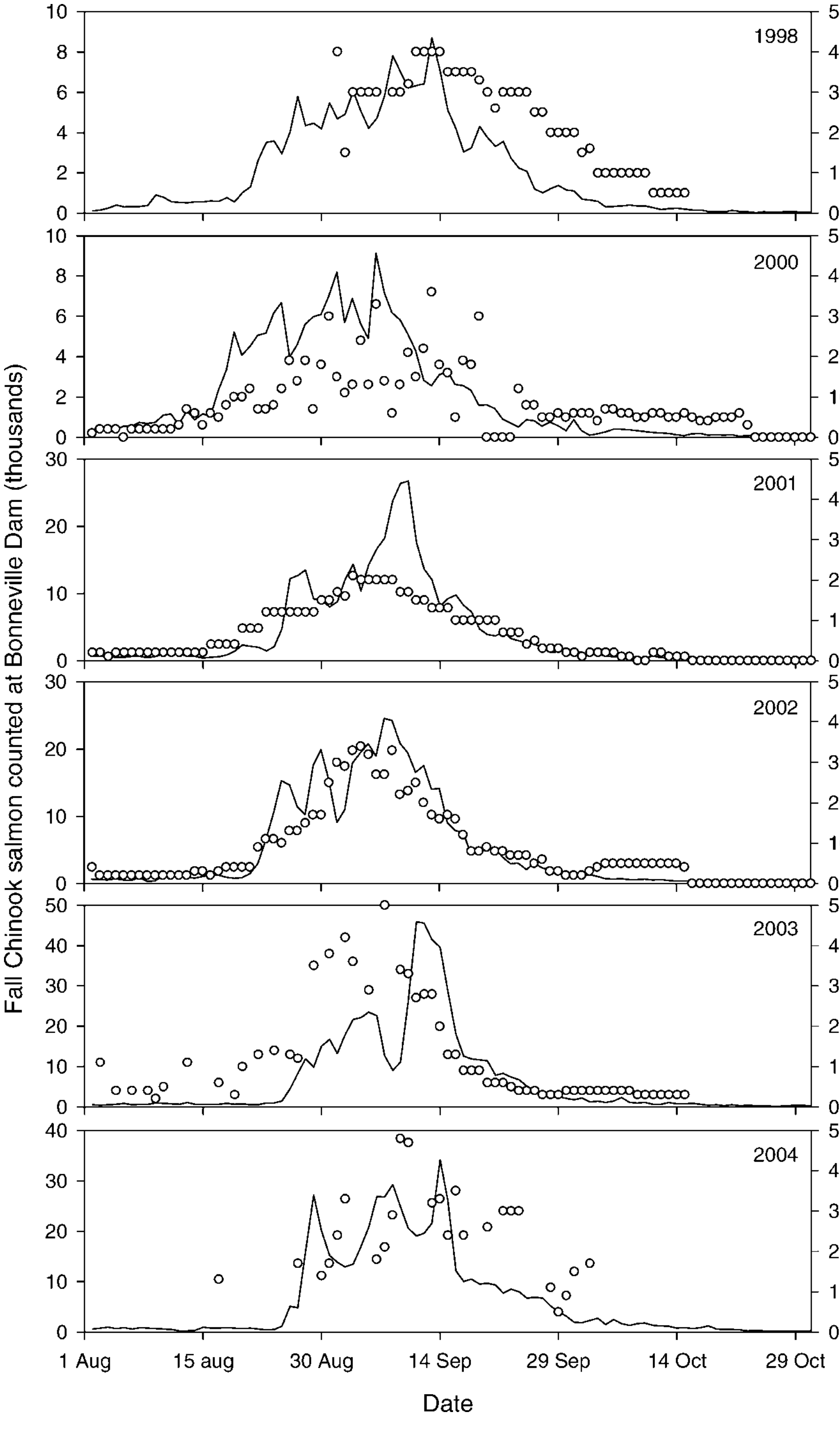

FIGURE 2.—Numbers of fall Chinook salmon counted by the U.S. Army Corps of Engineers at Bonneville Dam (solid lines) and daily numbers of salmon collected, radio-tagged, and released downstream from the dam (circles) in 1998 and 2000–2004.

Granite and Priest Rapids dams. Additional underwater antennas monitored fish passage in dam fishways and at ladder exits. Receivers recorded transmitter frequency and code plus date, time, and signal strength. All tributaries in the Bonneville and the Dalles reservoirs also had fixed aerial antennas except Herman and Eagle creeks. Tributary antennas were placed upstream from confluences to monitor fish that exited the Columbia River; sites were far enough upstream to minimize detection of fish passing in the main-stem Columbia River. Periodic mobile tracking with boat- and truck-mounted antennas supplemented the fixed-site data. Herman and Eagle creeks were not monitored continuously, and therefore data from those two tributaries were not included in analyses. The entire river from the Bonneville Dam tailrace to Ice Harbor and Priest Rapids dams was tracked by boat or truck at the end of each field season to assess final fish locations.

Data analysis.—Migration rates (km/d) through the lower Columbia River were calculated using telemetry records of each radio-tagged fish recorded at fixed sites at both Bonneville Dam (top of ladder sites) and John Day Dam (fishway entrance sites), a distance of about 111.8 km. Only fish that passed John Day Dam were included as this group was assumed to best represent URB fish. The time radio-tagged salmon spent in continuously monitored tributaries to the Bonneville Reservoir (Wind, Little White Salmon, White Salmon, Hood, and Klickitat rivers) and in the Deschutes River was calculated from the first to last telemetry records at those sites. Multiple times were calculated and summed for fish that exited and reentered one or more tributaries. For analyses, salmon were considered to have "used" tributaries if their cumulative total time in tributaries was greater than 12 h. Data from aerial antennas near tributary mouths but on the main-stem Columbia River indicated that some fish used portions of tributaries downstream from tributary antenna sites as well as tributary plumes within the Columbia River itself, but we did not include these times as antenna coverage was inconsistent between sites. Similarly, detections of salmon with mobile gear in Herman and Eagle creeks were not included because residence times could not be calculated. Our estimates of tributary use should therefore be considered minimums.

Mean daily water temperatures for the main-stem Columbia River were collected by USACE at the water quality monitoring site in the forebay of Bonneville Dam (archived at http://www.cqs.washington.edu/dart). Between-year temperature differences were assessed for each month (August–October) using analysis of variance (ANOVA). We also collected hourly temperature data in six major tributaries (Wind, Little White Salmon, White Salmon, Hood, Klickitat, and Deschutes rivers) in August and September. These monitoring sites were upstream from confluences with the Columbia River, but two (Little White Salmon and White Salmon) were located in areas where tributary and Columbia River water mixed; we note that these tributaries were much cooler upstream from the mixing zone. As an index of main-stem water temperature exposure we used weekly mean Columbia River temperatures for each radio-tagged salmon based on the date of fish passage at Bonneville Dam. We believe weekly means were more appropriate than daily means given the variability in transit times through the lower river (see Results).

The relationships between Columbia River temperature and salmon migration rates (log transformed) were assessed using multivariate general linear models (GLM) stratified by year and temperature category (1°C increments). This model structure (migration rate = year + temperature + [year × temperature]) allowed us to identify potential temperature thresholds and to control for some environmental differences among years. Year and interaction effects were expected given annual temperature differences and differences in tagging effort among years. We examined temporary tributary use (>12 h) using multiple logistic regression (use [0, 1] = temperature + year + [year × temperature], with temperature as a continuous variable; Allison 1999). We further tested whether radio-tagged fish that used tributary streams for more than 12 h had slower migration rates than fish that did not use tributaries using Kruskal–Wallis tests, and if migration rates for salmon that did or did not use tributaries differed among years using ANOVA.

Results

Water Temperatures

Columbia River water temperatures were greater than 20°C and as high as 23°C through most of August in all years and then steadily cooled through September and October (Figure 3). Mean temperatures differed significantly between years for August (df = 5; $F = 59.70$; $P < 0.0001$), September (df = 5; $F = 18.23$; $P < 0.0001$), and October (df = 5; $F = 6.06$; $P < 0.0001$). Pairwise comparisons indicated that August temperatures were highest in 1998, 2003, and 2004; September was warmest in 1998 and 2003; and October was relatively warm in 2003 and 2004 (Table 1). Mean daily tributary temperatures were approximately 2° to 7°C cooler than the main-stem Columbia River during both August and September (Figure 4).

Migration Rates

A total of 2,121 radio-tagged fall Chinook salmon passed John Day Dam and had telemetry records at

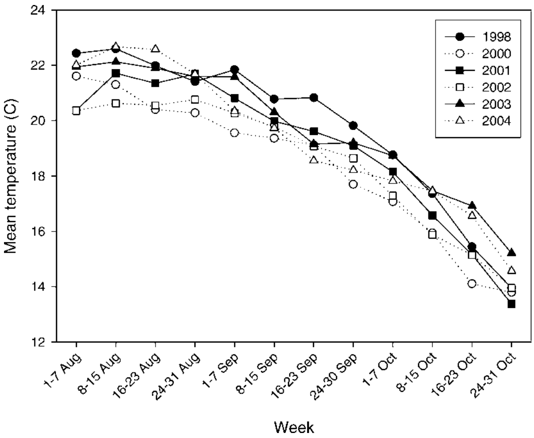

FIGURE 3.—Mean weekly water temperatures in the lower Columbia River as recorded at Bonneville Dam, 1998 and 2000–2004.

both the top of Bonneville Dam and at the John Day Dam fishway. Migration rates for these fish ranged from 1.8 to 75.5 km/d (mean = 34.4; median = 37.5; SD = 14.6). Weekly median passage rates were mostly between 30 and 45 km/d when Columbia River temperatures were below 21°C, and then decreased by approximately 50% at higher temperatures (Figure 5). In the multivariate GLM, temperature was the most influential predictor of migration rates (df = 7; sum of squares [SS] = 33.51; $F = 15.69$; $P < 0.0001$) followed by year (df = 5; SS = 9.27; $F = 6.07$; $P < 0.0001$) and the year × temperature interaction term (df = 18; SS = 26.54; $F = 4.83$, $P < 0.0001$). Pairwise Tukey's tests indicated that salmon migrated more slowly at higher temperatures and in warmer years (Table 2). The significant interaction term suggests that the effect was greater in some years, likely reflecting both sampling and temperature differences among years (i.e., salmon were not monitored across all temperature categories in all years).

As would be expected, salmon that used tributaries for more than 12 h had significantly slower (Kruskal–Wallis tests: $P < 0.0001$) migration rates in all years than fish that did not use tributaries. Migration rates for salmon that did not use tributaries differed significantly among years (ANOVA: df = 5; SS = 11.95; $F = 10.71$; $P < 0.0001$), with slower rates in warmer years consistent with the overall sample (Tukey's tests). Rates also differed among years for those fish that did use tributaries (df = 5; SS = 7.1; $F = 4.00$; $P = 0.0018$), though only one pairwise difference was significant (salmon that used tributaries migrated more slowly in 1998 than in 2003).

TABLE 1.—Mean Columbia River water temperatures at Bonneville Dam during August, September, and October. Within months, years with the same letter had significantly different mean temperatures in pairwise comparisons (Tukey's tests; $\alpha = 0.05$).

Year	August	September	October
1998	22.09 abc	20.81 abcde	16.30
2000	20.87 adef	18.95 afg	15.17 ab
2001	21.31 bdghi	19.87 bfh	15.74 c
2002	20.58 cgjk	19.44 c	15.46 d
2003	21.88 ehjl	20.04 dgi	17.03 acd
2004	22.24 fikl	19.21 ehi	16.56 b

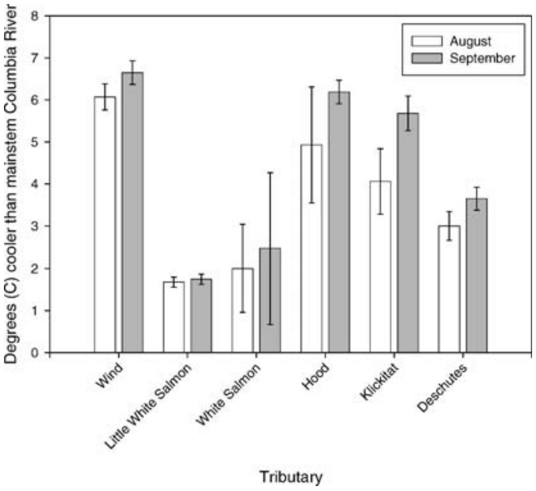

FIGURE 4.—Differences (°C; ±SD) between mean August and September water temperatures in the main-stem Columbia River and lower Columbia River tributaries, 1998 and 2000–2004 ($n = 6$ years for all but Little White Salmon and Klickitat rivers, where $n = 5$).

Tributary Use

Overall, 18% (379 of 2,121) of all radio-tagged salmon were recorded inside lower Columbia River tributaries prior to reaching John Day Dam and 9% (194 of 2,121) used tributaries for more than 12 h. Residence times for the latter group ranged from 12 h to 34 d (mean = 5.1 d; median = 2.9 d; SD = 5.8 d). The Little White Salmon and White Salmon rivers were most used, followed by the Deschutes and Klickitat rivers. Antennas near the mouths of the Wind and Deschutes rivers also indicated that many fish used the plumes from these rivers without being recorded upstream. The proportions of salmon that used tributaries increased exponentially with increasing mean weekly Columbia River water temperature, from mostly less than 5% when temperatures were below 20°C to about 40% when temperatures neared 22°C (Figure 6). The likelihood of temporary tributary use increased significantly as Columbia River temperature increased (multiple logisitic regression: $\chi^2 = 88.12$; P

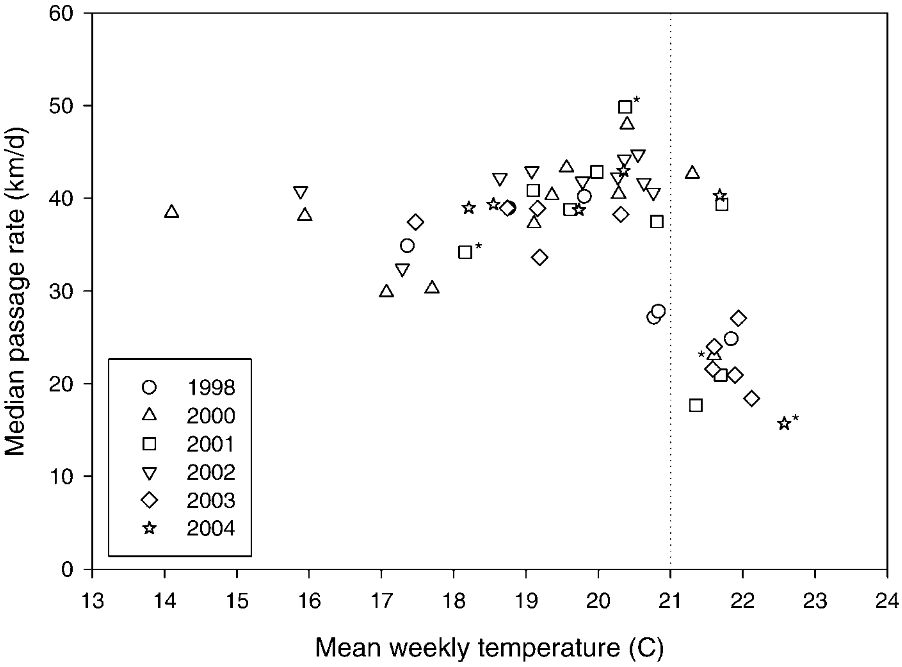

FIGURE 5.—Relationship between median fall Chinook salmon migration rates (Bonneville Dam to John Day Dam) and mean weekly water temperatures at Bonneville Dam. Symbols represent 52 weekly bins (mean = 41 fish/bin; range = 4–122 fish/bin). Asterisks indicate data points with fewer than 10 fish.

< 0.0001), and more salmon used tributaries in warm years ($\chi^2 = 27.15$; $P < 0.0001$). The year × temperature term was not significant ($P = 0.822$), indicating that the temperature effect did not differ among years; this term was dropped from the model.

TABLE 2.—Fall Chinook salmon migration rates (km/d; CI = confidence interval) from Bonneville Dam to John Day Dam by temperature interval at Bonneville Dam and migration year. Data were back-transformed from natural logarithms. Factors with common letters were significantly different in pairwise comparisons (Tukey's tests; $\alpha = 0.05$).

Factor	Mean	95% CI
Temperature interval		
14–14.9	32.4	24.3–43.3
15–15.9	37.6	30.7–45.9 ab
16–16.9		
17–17.9	29.0	25.9–32.5 cdef
18–18.9	36.5	33.7–39.5 cghi
19–19.9	36.6	35.1–38.2 djkl
20–20.9	30.6	29.3–31.9 gjmn
21–21.9	22.0	20.7–23.3 aehkm
22–22.9	18.1	14.0–23.4 bfiln
Year		
1998	25.0	23.7–26.5 abcd
2000	34.7	32.7–36.9 ae
2001	29.0	27.2–31.0 befg
2002	37.0	34.9–39.3 cfh
2003	27.3	25.6–29.0 ehi
2004	35.1	32.9–37.4 dgi

Historical Run Timing

Count data at Bonneville and McNary dams suggest that fall Chinook salmon run timing distributions have shifted through time from high, compressed peaks in counts to somewhat flatter distributions with more early and late migrants. At both dams, first quartile passage dates have become significantly ($P < 0.05$) earlier over time and third quartile dates have become later ($P < 0.05$), resulting in increasing (linear regression: $P < 0.0001$) interquartile ranges (Figure 7). Interquartile ranges have increased from about 7 to 14 d (100%) at Bonneville Dam and from about 11 to 18 d (64%) at McNary Dam. Regression slopes suggest that the rate of change has been more rapid at McNary Dam. Patterns were similar, though not significant ($P > 0.05$), at John Day Dam. Count data at the Dalles Dam were missing or incomplete from 1960 to 1976, and regression analyses of the truncated data set (1977–2004) indicated no significant ($P > 0.05$) trends. Notably, we did not detect changes in median passage dates over time at any dam.

Discussion

As would be expected for a coldwater fish species, we found some strong associations between Columbia River water temperature and adult fall Chinook salmon migration behaviors. The radiotelemetry data con-

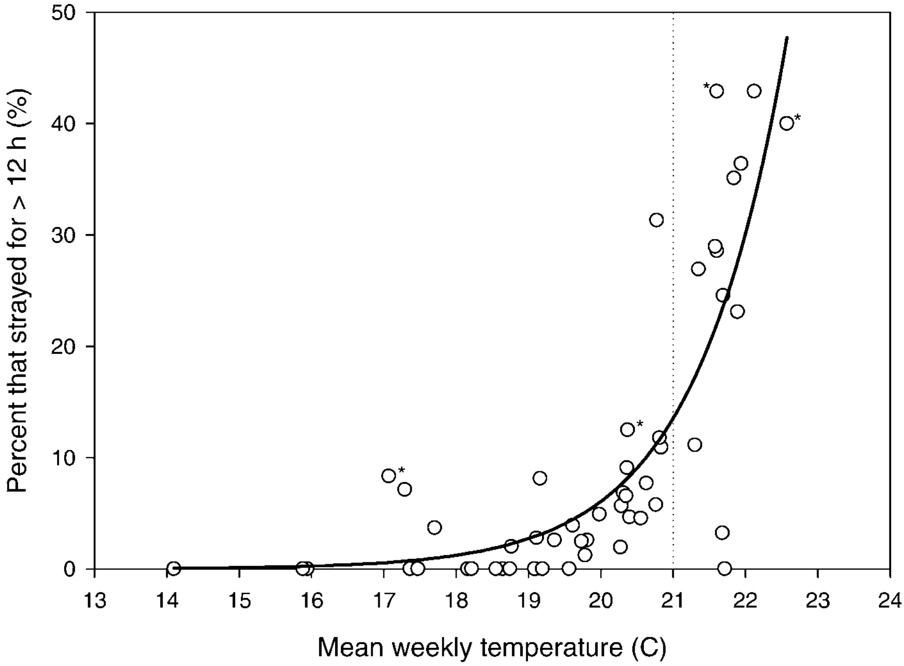

FIGURE 6.—Relationship between the percent of fall Chinook salmon that used (>12 h) coolwater tributaries and mean weekly water temperatures at Bonneville Dam. Circles represent 52 weekly bins (mean = 41 fish/bin; range = 4–122 fish/bin). The curve is the exponential regression line that best fits the data ($r^2 = 0.80$; $P < 0.0001$; percent = $6.558^{-7}e^{0.802\times\text{temperature}}$). Asterisks indicate data points with fewer than 10 fish.

firmed that a portion of adult salmon homing to upstream locations slowed or stopped migrating in the lower Columbia River during warm river conditions. Many of the telemetered fish strayed temporarily into cooler tributary rivers, and the strength of this response increased both within and among years as water temperatures increased. Use of coolwater streams clearly signals active behavioral thermoregulation, and our methodology may have captured only a fraction of this activity. For example, many fish used cool tributary plumes, others were recorded in tributaries that were not continuously monitored (e.g., Eagle and Herman creeks), and some likely used deep refugia or other coldwater sites (i.e., springs), although the existence of the latter have not been documented in the lower Columbia River study area. Below we discuss the implications of these thermoregulatory behaviors, the potential for fall Chinoook salmon run timing and migration plasticity, and the importance of maintaining thermal refugia.

Although many fall Chinook salmon in this study had thermoregulatory behaviors during migration, it is important to note that not all fish responded to warm Columbia River temperatures in the same way. We had expected a slowing of migration activity when mean water temperatures reached levels we considered suboptimal (>20°C) and to decline sharply or even halt upon reaching sublethal levels (22–24°C), but this did not occur. Instead, even during warm years and warm periods, a majority of fall Chinook salmon continued to migrate through presumably stressful

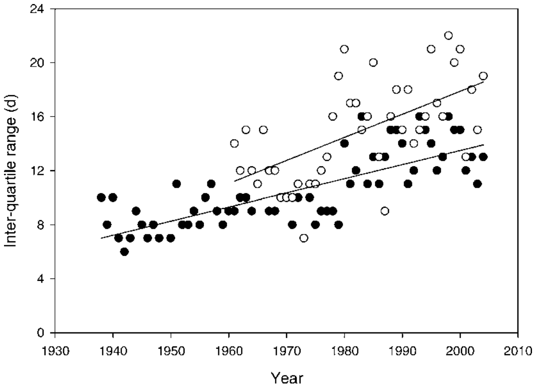

FIGURE 7.—Relationship between migration year and the interquartile range of fall Chinook salmon passage dates at Bonneville Dam (solid circles; range = [0.10 × year] – 195.2; $r^2 = 0.59$; $P < 0.0001$) and McNary Dam (open circles: range = [0.17 × year] – 324.2; $r^2 = 0.36$; $P < 0.0001$).

water temperatures. There are several potential explanations for this. One is that we did not correctly or completely identify the thermal environments salmon used. The tagged fish certainly encountered water temperatures during migration that varied significantly (higher and lower) from those collected at the water quality monitoring site. Ongoing studies with salmon outfitted with archival temperature recorders will help address this variability and uncertainty. We believe a more compelling explanation for continued migration during potentially stressful conditions was that fall Chinook salmon have a relatively short window in which to migrate prior to the onset of spawning at upstream areas. The imperative of reaching spawning grounds at appropriate times may have prompted adult salmon to continue migration even when temperature conditions were suboptimal. This behavior contrasts with that from similar analyses for adult steelhead *O. mykiss*, where we found stronger relationships between temperature, passage rates, and the proportions of radio-tagged fish that temporarily entered lower river tributaries (Keefer et al. 2004a; High et al., in press).

Associations between water temperature and salmonid distributions and behaviors have been relatively well-studied because of the species' commercial, recreational, and ecological importance. For example, resident adult trout are known to seek coolwater refugia in streams (Kaya et al. 1977; Biro 1998; Baird and Krueger 2003) and lakes (Snucins and Gunn 1995). Adult anadromous salmonids can be temperature selective in the ocean (chum salmon *O. keta*; Tanaka et al. 2000) and while holding in spawning and prespawning areas (Chinook salmon: Berman and Quinn 1991; Torgersen et al. 1999; Newell and Quinn 2005; steelhead: Nielsen et al. 1994). The current results strongly suggest that actively migrating adult salmon also select for optimal temperatures. The results also suggest an apparent threshold temperature for Columbia River fall Chinook salmon between 20°C and 21°C, above which many fish seek refugia or reduce migration activity. A similar threshold has been identified for Columbia River sockeye salmon *O. nerka* (Hyatt et al. 2003).

Previous studies suggest that the timing of river entry and migration for anadromous salmonids is selectively adapted (Smoker et al. 1998; Quinn et al. 2000, 2002; Stewart et al. 2002; Keefer et al. 2004b). And although some stocks, particularly steelhead, have some flexibility with which to react to prevailing river flow and temperature conditions (Robards and Quinn 2002; Keefer et al. 2004a), flexibility in migration timing generally appears to be limited for salmonids. Quinn and Adams (1996) observed that return timing for Columbia River sockeye salmon was less variable over time than for nonindigenous American shad *Alosa sapidissima*, and suggested that migration timing for sockeye salmon was less plastic than for the introduced species and did not match the rate of environmental change. Our fall Chinook salmon run timing analysis suggests that fall Chinook salmon have also responded, but only moderately, to the warming Columbia River environment. The modest increases in the proportions of fall Chinook salmon arriving both earlier and later than historically noted may reflect some behavioral plasticity. However, the fact that median dates have remained relatively unchanged suggests that, on average, this run has probably been exposed to increasingly warmer water temperatures over time. The implications of this for survival, energetic demands, and gamete development are unclear, though exposure to high temperatures during migration has been associated with elevated bioenergetic depletion and prespawn mortality (Gilhousen 1990; Cooke et al. 2004; Naughton et al. 2005; Richter and Kolmes 2005) and lowered fertility (Flett et al. 1996; King et al. 2003) in other salmon runs.

Because the current Columbia River environment will probably assure continued use of lower river tributaries by adult migrants, attention should be focused on maintaining favorable thermal conditions and refugia within these rivers. During the warmest periods, large numbers of salmon can be expected to concentrate in tributary streams where they may be exposed to terminal fisheries. This may be especially relevant for Snake River fall Chinook salmon, which are listed as threatened under the Endangered Species Act and for which reduced survival in the migration corridor could have significant population-level impacts. The predicted rise in global temperature from 2°C to 5°C over the next century (Neitzel et al. 1991; Hamlet and Lettenmaier 1999), combined with warming due to impoundment and water diversion (Quinn et al. 1997), suggests Columbia River temperatures will continue to rise. It is possible this trend may be tempered through managing the system to more closely mimic natural flow patterns (e.g., Postel and Richter 2003). However, the ability of fall Chinook salmon and other migratory stocks to adjust to increasing temperatures may determine their ability to persist in the Columbia River and elsewhere.

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Appendix Follows

Appendix: Regression Results

Table A.1.—Linear regression relationships between year and fall Chinook salmon run timing metrics based on available U.S. Army Corps of Engineers counts at ladders at Bonneville (1961–2004), the Dalles (1977–2004), John Day (1969–2004), and McNary (1961–2004) dams. Years with incomplete count data were excluded.

Dam	Timing metric	r^2	Slope	*P*
Bonneville	1st quartile date	0.08	−0.0379	0.0288
	Median date	0.00	0.0069	0.6537
	3rd quartile date	0.26	0.0664	<0.0001
	Interquartile range	0.59	0.1044	<0.0001
The Dalles	1st quartile date	0.06	−0.0821	0.2204
	Median date	0.11	−0.1169	0.0860
	3rd quartile date	0.06	−0.0837	0.2276
	Interquartile range	0.00	−0.0016	0.9749
Jahn Day	1st quartile date	0.08	−0.0869	0.1133
	Median date	0.02	−0.0637	0.1935
	3rd quartile date	0.00	0.0096	0.8645
	Interquartile range	0.12	0.0965	0.0526
McNary	1st quartile date	0.09	−0.0756	0.0459
	Median date	0.00	−0.0001	0.9971
	3rd quartile date	0.14	0.0954	0.0117
	Interquartile range	0.36	0.1710	<0.0001